Integrating Genetic, Environmental, and Social Networks to Reveal Transmission Pathways of a Dolphin Foraging Innovation

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Abstract: Cultural behavior, which is transmitted among conspecifics through social learning [1], is found across various taxa [2 , 3 , 4 , 5 , 6]. Vertical social transmission from parent to offspring [7] is thought to be adaptive because of the parental generation being more skilled than maturing individuals. It is found throughout the animal kingdom, particularly in species with prolonged parental care, e.g., [8 , 9]. Social learning can also occur among members of the same generation [4 , 10 , 11] or between older, non-parental individuals and younger generations [7] via horizontal or oblique transmission, respectively. Extensive work on primate culture has shown that horizontal transmission of foraging behavior is biased toward species with broad cultural repertoires [12] and those with increased levels of social tolerance [13 , 14], such as great apes. Vertical social transmission has been established as the primary transmission mechanism of foraging behaviors in the Indo-Pacific bottlenose dolphin (Tursiops aduncus) population of Shark Bay, Western Australia [6 , 9 , 15 , 16]. Here, we investigated the spread of another foraging strategy, "shelling" [17], whereby some dolphins in this population feed on prey trapped inside large marine gastropod shells. Using a multi-network version of "network-based diffusion analysis" (NBDA), we show that shelling behavior spreads primarily through non-vertical social transmission. By statistically accounting for both environmental and genetic influences, our findings thus represent the first evidence of non-vertical transmission of a foraging tactic in toothed whales. This research suggests there are multiple transmission pathways of foraging behaviors in dolphins, highlighting the similarities between cetaceans and great apes in the nature of the transmission of cultural behaviors.

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Integrating genetic, environmental and social networks to reveal transmission pathways of a dolphin foraging innovation

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22 Social learning, network-based diffusion analysis, NBDA, animal culture, dolphins, horizontal
23 learning, non-vertical learning, foraging, tool use

SUMMARY

Cultural behavior, that transmitted among conspecifics through social learning [1], is found across various taxa [2–6]. Vertical social transmission from parent to offspring [7] is thought to be adaptive because of the parental generation being more skilled than maturing individuals. It is found throughout the animal kingdom, particularly in species with prolonged parental care e.g. [8,9]. Social learning can also occur among members of the same generation [4,10,11] or between older, non-parental individuals and younger generations [7] via horizontal or oblique transmission, respectively. Extensive work on primate culture has shown that horizontal transmission of foraging behavior is biased toward species with broad cultural repertoires [12], and those with increased levels of social tolerance [13,14], such as great apes. Vertical social transmission has been established as the primary transmission mechanism of foraging behaviors in the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) population of Shark Bay, Western Australia [6,9,15,16]. Here, we investigated the spread of another foraging strategy, 'shelling' [17], whereby some dolphins in this population feed on prey trapped inside large marine gastropod shells. Using a multi-network version of 'network-based diffusion analysis' (NBDA), we show that shelling behavior spreads primarily through non-vertical social transmission. By statistically accounting for both environmental and genetic influences, our findings thus represent the first evidence of non-vertical transmission of a foraging tactic in toothed whales. This research suggests there are multiple transmission pathways of foraging behaviors in dolphins, highlighting the similarities between cetaceans and great apes in the nature of the transmission of cultural behaviors.

RESULTS AND DISCUSSION

During boat-based surveys in the western gulf of Shark Bay (Figure 1) between 2007 and 2018, we identified 1,035 different individuals from 5,278 dolphin group encounters. A total of 42 shelling events (Video S1) was documented during this period (Figure 1), performed by 19 individual dolphins from three different mitochondrial DNA (mtDNA) haplotype lineages (haplotype hereafter). Although shelling appears quite rare, both the number of shelling events and the number of individual 'shellers' is an underestimate, as the behavior occurs in bouts lasting a few seconds, and is therefore hard to observe. To maximize power of NBDA to detect social transmission, we used a simulation approach [18] to identify an appropriate minimum threshold for the inclusion of individuals, which, for this data set, was 11 sightings (see STAR methods). A total of 310 individuals with at least 11 sightings each remained for analyses, of which 15 were shellers (six females; nine males).

NBDA supports non-vertical social transmission among associates

To investigate the different pathways of transmission of shelling, we ran a multi-network version of the 'order-of acquisition diffusion analysis' (OADA) variant of NBDA [19]. NBDA infers social transmission if the diffusion of a behavior follows the social network [20,21]. Going beyond previous studies on social transmission, e.g. [6,22], we also incorporated environmental and genetic factors, as these could plausibly result in patterns that superficially resemble social transmission [23] (see STAR methods).

We included three different networks, namely an association network modelling social transmission, a network with home range overlaps as a proxy for environmental similarity, and a network with pairwise genetic relatedness based on autosomal markers among individuals to test for a hypothetical genetic predisposition for shelling. We ran models with and without transmission along all possible combinations of the three networks, and used the Akaike Information Criterion corrected for sample size (AICc) to obtain relative model support [24]. Results of OADA revealed most relative support for models including only the association network ($\sum w_i = 0.771$; Figure 2), which modelled

social transmission. In contrast, models with asocial learning or all other network combinations received little support ($\sum w_i < 0.1$; Figure 2), indicating that social transmission was 10-320 times more likely than any other pathway including asocial learning, and combinations of genetic and/or environmental factors. Note that social transmission includes transmission among associated individuals, which could be both horizontal and oblique, but will be referred to as 'non-vertical transmission' hereafter, as in any social learning outside of the mother-calf bond.

Estimating the strength of social transmission

In an NBDA, the strength of social transmission is estimated as the parameter *s*: defined as the rate of transmission per unit connection with informed individuals, relative to a baseline rate of asocial learning (set to be the asocial learning rate for individuals with haplotype E; see STAR methods). For an individual with average group size (= each individual's average number of group members averaged across the population), *s* was estimated to be 15.6 [95% C.I. 2.06-145], indicating a 15.6-fold increase in the social learning rate per unit connection with informed individuals relative to the baseline level of asocial learning. This corresponds to an estimated 57% [95% C.I. 41%-74%] of dolphins learning shelling by social transmission. The estimated strength of social transmission stayed the same even if the environmental and/or genetic network were added to the best model.

Effects of individual-level variables (ILVs) on social transmission

We also estimated the effect other variables had on *s*. Average group size affected social transmission ($\sum w_i$ = 0.629), estimating that, for every added associate, the value of *s* decreased by a factor of 2 [95% C.I. 1.18-3.91]. This may be because dolphins that tended to spend time in larger groups had their attention divided among more associates, and thus learned at a lower rate per unit of association. None of the other individual-level variables (ILVs) we tested (sex, number of sightings, average water depth, haplotype) had an influence on an individual's social transmission rate (all $\sum w_i$ <0.5; see STAR methods and Table 1).

Effects of individual-level variables (ILVs) on asocial learning

We further estimated the influence of ILVs on the asocial learning rate. Individuals with haplotype D and E were more likely to acquire shelling independent of the social network, while none of the other ILVs (sex, number of sightings, average water depth, average group size) had an influence on the asocial learning rate (Table 1). Dolphins with haplotype D were an estimated 47.1 [95% C.I. 5.6-303] times faster to learn than those with haplotype E, whilst dolphins with haplotype E were an estimated $1.5x10^9$ [95% C.I. 3.1-Inf] times faster to learn than those of other haplotypes. These inferences are largely influenced by the fact that *hitherto* only dolphins of haplotypes D and E have learned shelling while having no social network connections to other shellers (3 individuals). Given the limited sample size, the large estimates of the size of this effect are unlikely to be accurate. However, the 95% confidence intervals provide a reasonable lower limit for the effect.

Social transmission of shelling among associates

Multi-network NBDA revealed most support for a transmission pathway of the foraging technique shelling among associated dolphins, providing the first quantitative evidence of a non-vertically transmitted foraging behavior in a toothed whale species, while also statistically controlling for genetic and environmental influences. Our results do not distinguish between horizontal and oblique transmission, but include all non-vertical social transmission outside of the mother-calf bond. These results are surprising, insofar as vertical social transmission between mother and offspring has been established as the primary mechanism for foraging behaviors in Shark Bay's dolphins e.g. [6,9,15] and, in fact, toothed whales in general e.g. [25–29]. Close proximity between mother and offspring during dependency combined with prolonged parental care provides ample opportunities for social transmission of behavior, explaining the prevalence of vertical transmission [9,30]. Our results quantify non-vertical transmission of shelling, however, illustrating that free-ranging dolphins are also capable of learning foraging behavior outside the mother-calf bond. This builds upon previous cases of presumed horizontal transmission of behavior in toothed whales that were descriptive or anecdotal in nature [31–33]. Social learning opportunities increase with the duration and frequency

of proximity between demonstrator and observer [34]. Both females and, in particular, allied male dolphins in Shark Bay show high levels of social tolerance within cohesive social groups [35–37], which manifests itself in spatial proximity during foraging and we hypothesize may have facilitated the horizontal spread of shelling.

Our results further illustrate that dolphins were not only capable but also motivated to learn from others. Prior research on this population suggested that dolphin calves primarily followed their mothers in adopting the techniques requiring high levels of specialization: the use of sponges as foraging tools ('sponging'), for example [38,39], which is transmitted vertically from mother to primarily female offspring [6,40,41]. Offspring tend to incorporate their mothers' home range into their own [42], which warrants selection for the same foraging specializations [9]. As such, and in order to avoid acquiring unsuitable or even maladaptive behavior, calves tend to follow a do-as-mother-does strategy for specialized strategies [9]. Shelling, however, occurs on an opportunistic basis, with all shellers also engaging in other strategies, and does not appear to require the same level of specialization. This reduces the potential costs associated with learning a new foraging behavior, and may thereby facilitate the horizontal or oblique spread of shelling.

Highly specialized foraging techniques such as sponging tend to be biased towards females due to sex-specific reproductive strategies, differing between male and female dolphins. Male dolphins in Shark Bay must invest in the formation of alliances with other males to coerce and consort oestrous females [36,43,44], which is time-consuming and therefore largely incompatible with highly specialized and spatially restricting behaviors such as sponging [39,45], but see [46]. This may explain the lack of a sex-bias in shelling, as both sexes can equally afford to engage in the behavior.

In our analyses, we included an individual's haplotype as a statistical control to account for a potential role of vertical social transmission (see STAR methods). The propensity of dolphins with haplotypes D and E to exhibit shelling could be taken as evidence of an association of shelling with particular matrilines and, therefore, evidence for vertical social transmission. However, given small

sample sizes, the importance of a potential role of vertical learning and the size of the potential effects of haplotypes cannot be estimated reliably at this stage. Importantly, our analysis shows that haplotype and, with it, vertical social learning does not sufficiently explain the pathway of diffusion, and when controlling for it, there is still a sizable effect of the social network. Even if a potential role of vertical learning cannot be fully excluded, there is still strong evidence for a substantial non-vertical social transmission effect.

Our best model indicated that approximately 43% of the dolphins learned shelling independent of the social network, *i.e.*, through asocial learning. Given that bottlenose dolphins are cognitively-advanced animals capable of behavioral innovation [47], it is plausible that some individuals may have acquired shelling independently. However, due to the limited number of observations of those individuals, it may also be that we failed to capture some of the connections with other shellers in our dataset. In this context, it is worth noting that sponging appears to have arisen independently in each gulf of Shark Bay [48], highlighting the potential for complex behavioral innovations in this population.

Another innovation involving tool use

Along with sponging [6,9,49], shelling represents only the second reported case of tool use in dolphins. To qualify as tool use, a behavior must involve the external employment of an unattached environmental object; serve to alter the form, position or condition of another object, organism or the user itself; and the user must be responsible for the proper and effective orientation of the tool [50]. Dolphins utilize the shell to first entrap the prey before exposing it to gravity by lifting the shell above the water surface and shaking it about in order to dislodge the prey, thereby fulfilling these conditions and qualifying shelling as tool use.

Cultural transmission pathways in rapidly changing environments

Theory predicts that stable environments should favour cultural conservatism: The reliance on already established information obtained from older generations through vertical or oblique transmission is thought to be advantageous because it is tested, experience-based and thus most

likely adapted to current environmental conditions [31]. Rapid environmental change, however, should favour cultural progressivism through horizontal transmission, as information can become out-dated, promoting the acquisition of innovative behavior from conspecifics in order to adapt quickly to novel ecological conditions [31]. An unprecedented marine heatwave in 2011 caused catastrophic seagrass die-off and subsequent ecological disturbance across trophic levels in Shark Bay [51–53], with long-term negative impacts on survival and reproduction in the dolphin population [54]. Interestingly, shelling occurred more frequently immediately following the heatwave, with more than 50% of all shelling events being observed in the two years subsequent to the heatwave (data not shown). While we can only speculate as to whether the extreme event has selected for horizontal transmission to adapt to the rapidly changing conditions, it seems conceivable that an abundance of dead or dying giant gastropods following the heatwave may have increased learning opportunities for shelling behavior.

Similarities in cultural nature between cetaceans and great apes

It is generally beneficial for dependent individuals to rely on social information to first acquire novel skills, though the benefits of acquiring new behavior from others are thought to decrease as maturing individuals become more proficient themselves [12]. Nevertheless, learning from others can continue into adulthood, and tends to occur in species with extensive cultural repertoires, *i.e.*, a broad range of socially learned behaviors, and those characterized by high levels of social tolerance, such as great apes [12,14]. Evidence for non-vertical social transmission of shelling among adult dolphins thus sets an important milestone, and suggests that the cultural natures of great apes and dolphins are similar. Indeed, despite having divergent evolutionary pathways and occupying markedly disparate environments (terrestrial versus aquatic), some great apes and dolphins show striking similarities in cognitive abilities, life history characteristics and social systems: they are long-lived, large-brained mammals with high capacities for innovation [47,55–57]. Furthermore, many dolphin species live in fission-fusion societies e.g. [58], similar to those found in chimpanzees, for example [59]. Many of these societies, at least within social units such as dolphin alliances or

chimpanzee communities, are generally characterized by high levels of social tolerance, providing many opportunities for social interactions, thought to be an important predictor of social learning rates of foraging behavior [12,14].

We present the first quantitative evidence of a significant role for non-vertical social transmission of a foraging behavior, shelling, in any toothed whale species, in which we have statistically controlled for alternative transmission pathways (genetic and/or environmental). Our research, when combined with evidence from previous studies, suggests multiple pathways of transmission of foraging behaviors in dolphins (both vertical and non-vertical), highlighting the similarities between the cultural natures of cetaceans and great apes.

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Author contributions

MK, SA and SW conceived the study. SW and WH conducted statistical analyses. SW collected data and drafted the manuscript. MK secured funding. SA collected data. All authors contributed to writing.

Declaration of interests

The authors declare no competing interests.

Figure Legends

Figure 1: GPS locations of dolphin group sightings and shelling events. Over 5,300 dolphin groups (blue triangles) and 42 shelling events (yellow triangles) were observed between 2007 and 2018 in western Shark Bay. As shelling behavior occurs in bouts of short duration, the observed number is likely an underestimate.

Figure 2: Relative support for the diffusion of shelling along different pathways. Multi-network NBDA revealed most support for transmission of shelling along the association network (modelling social transmission), while asocial learning, and any combination of environmental and/or genetic networks received little support.

230 **Table 1: Support for ILVs and model average estimates as weighted medians**

ILV	Sex	Number of sightings	Average water depth	Average group size	Haplotype
Relative support for effect on social learning	0.136	0.108	0.119	**0.629**	0.025
Model averaged estimate (back-transformed)	-	-	-	x1.99 per associate	-
Profile likelihood confidence interval conditional on the best model	-	-	-	[1.18-3.91] per associate	-
Relative support for effect on asocial learning	0.199	0.097	0.444	0.093	**0.973**
Model averaged estimate* (back-transformed)	-	-	-	-	E/others: 1.46E9 D/others: 41.7
Profile likelihood confidence interval conditional on the best model	-	-	-	-	E/others: [3.1-Inf] D/others: [5.6-303]

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STAR Methods

Resource Availability

Lead Contact

All requests for further information on data or codes should be directed to, and will be fulfilled by, the Lead Contact, Sonja Wild (swild@ab.mpg.de).

Materials Availability

This study did not generate new unique reagents.

Data and Code Availability

The datasets generated during this study are available in the electronic supplementary material (Data S1 A-D). The R code for application of NBDA and extraction of profile likelihood intervals is available under [60].

Experimental Model and Subject Details

For this study, we observed free-ranging Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the western gulf of Shark Bay, Western Australia. Small tissue samples of dolphins were obtained using a remote biopsy system. Permits for the use of animals for scientific purposes were granted by the Department of Biodiversity, Conservation and Attractions (SF002958; SF010888; SF10388; SF002958; SF010774; 08-000920-1; 08-000706-3) and the Department of Agriculture and Food (U 10/2015-2018). The animal ethics committees of the University of Western Australia, Murdoch University and the University of Zurich provided approvals for the ethical treatment of animals in scientific research (R2649/14; RA/3/100/1449; RA/3/100/1464).

Method Details

Field methods

We collected data between 2007 and 2018 during boat-based surveys off the township of Useless Loop in the western gulf of Shark Bay, Western Australia (Figure 1), using standardized behavioral sampling methods [61]. On approach to each dolphin group, observers took a GPS location within 30 m of the initial sighting, and determined group composition using individual photo-identification [62]. All individuals within 10 m of any other dolphin (10 m chain rule) during the first five minutes of each encounter were considered part of the same group [63]. All occurrences of shelling behavior

(Video S1) were noted, including the identity of the individual performing the behavior. Given the distinctiveness of shelling and its obvious function, all individuals observed performing the behavior were considered 'shellers'. The small tissue (biopsy) samples were obtained on an opportunistic basis after five-minute behavioral surveys were completed, targeting individuals who had not been sampled yet. For biopsying, we used a modified 0.22 caliber rifle and polycarbonate biopsy darts with stainless steel tips, a system which was developed specifically for cetaceans [64]. Biopsy samples were stored in saturated NaCl/20% dimethyl sulphoxide solution (DMSO) [65] in the field at 4 °C and at minus 80 °C in the laboratory.

Genetic determination of biparental relatedness, mitochondrial matriline membership and sex

To control for the possibility that genetically related individuals might be similarly predisposed to learn shelling (see below), we estimated pairwise dyadic biparental relatedness between individuals.

For DNA extraction of tissue samples (N = 295), we used Qiagen's DNeasy kit and followed the manufacturer's protocol for minute samples and Qiagen's Gentra Puregene Mouse Tail kit for larger samples. We then determined DNA concentrations for each sample using NanoDrop 1,000 V3.3 (Technologies Inc. Wilmington, DE) and diluted the extracted DNA concentration to 20 ng/µl with DNA Hydration Solution (Qiagen).

To determine genotypes of sampled individuals, we amplified 27 microsatellite loci in three multiplex polymerase chain reactions (PCRs) (Table S1). PCRs contained 20 ng template DNA, 5 µL 2× Multiplex PCR Master Mix (QIAGEN, containing HotStarTaq DNA Polymerase, dNTPs and 3 mm MgCl2 final concentration), between 0.05 and 0.5 µm of each primer and double-distilled water to add up to a 10-µl volume. PCR amplifications were performed in a PTC-220 thermocycler (MJ Research) with the following profile: initial activation at 95 °C for 15 min, 25 cycles of 30 s at 95 °C, 90 s at 60 °C and 45 s at 71 °C, followed by a final extension step of 30 min at 60 °C. We diluted PCR products twenty-fold with ddH2O and added 1000 µl HiDi formamide plus 7 µl size standard (GenScanTM500LizTM, Applied

285 Biosystems). We analysed the PCR products via capillary electrophoresis using an ABI 3730 DNA
286 Sequencer (Applied Biosystems) and scored alleles with the GeneMapper 4.0 software (Applied
287 Biosystems).

288 We then calculated dyadic biparental relatedness based on the resulting genotypes for individuals
289 with no more than three loci missing (N = 293) using COANCESTRY v1.0.1.7 [66]. We obtained allele
290 frequencies for each locus (Table S1 and S2), missing and error rates (Table S1) from empirical data,
291 and used them as input parameters. Error rates were determined based on 29 individuals that had
292 been genotyped more than once. To determine which of the seven proposed relatedness estimators
293 performed best, we simulated 1,000 genotypes based on the allele frequency distribution in the
294 population (Table S2). Subsequently, we simulated 100 dyads each for half siblings (relatedness (r) =
295 0.25), parent-offspring (r = 0.5), full siblings (r = 0.5), first cousins (r = 0.125), and unrelated individuals
296 (r = 0). The estimator TrioML showed lowest variance (Table S3) and highest correlation with the true
297 data (Table S4), and was therefore chosen as the best performing estimator for this study population.
298 Using the empirical data, we then calculated relatedness for each dyad within the population using
299 TrioML. For dyads with no genetic information, we used the population average relatedness of 0.043
300 (Data S1 A).

301 Previous work on these dolphins provides evidence that foraging skills tend to be socially learned from
302 the mother [6,9]. As vertically transmitted foraging techniques within matrilines show an association
303 with haplotype, we included it as a factor in the analysis (further details below). To assign dolphins to
304 defined haplotypes [67], we sequenced a 468 bp-long fragment of the mtDNA (D-Loop), amplified by
305 the primers dlp1.5 and dlp5 [68]. PCRs contained 20 ng template DNA, 0.05 u Taq DNA Polymerase
306 (Sigma-Aldrich), 0.1 mM 170 dNTPs, PCR buffer, 0.13 MgCl2 mM final concentration, 0.1 µM of each
307 primer and double-distilled water to add up to a 20-µl volume. PCR amplifications were performed in
308 a PTC-220 thermocycler (MJ Research) with the following profile: initial activation at 94 °C for 3 min,
309 39 cycles of 45 s at 93 °C, 45 s at 52 °C and 60 s at 72 °C, followed by a final extension step of 10 min

310 at 72 °C. We purified PCR products using silica membrane spin columns (QIAquick®, Qiagen). The
311 sequences were aligned in BioEdit [69] and predefined haplotypes assigned by eye [67].

312 All individuals were also genetically sexed using sex chromosome-specific primers; loci ZFX and SRY
313 [70], coamplified in a single PCR. PCRs contained 20 ng template DNA, 0.15 µM of each primer, 0.1
314 mM dNTPs, 0.13 mM $MgCl_2$, 0.05 u Taq polymerase and double-distilled water to add up to a 10-µl
315 volume. PCR amplifications were performed in a PTC-220 thermocycler (MJ Research) with the
316 following profile: initial activation at 94 °C for 4 min, 40 cycles of 45 s at 94 °C, 45 s at 58 °C and 60 s
317 at 72 °C, followed by a final extension step of 10 min at 72 °C. PCR products were then run on a 1.5%
318 agarose gel and sex was determined based on the different fragments amplified, with females showing
319 one band and males showing two bands [70].

320 ## Inclusion of individuals

321 When using NBDA, there is a trade-off between sample size and data quality: excluding individuals
322 with only a few sightings can increase certainty about the strength of connections within the social
323 network but, at the same time, impact the power of NBDA to detect social learning if connecting
324 individuals are removed [18]. We therefore used a simulation approach to choose a cut-off point
325 that maximizes the power of NBDA to reliably detect social learning [18]. For computational reasons,
326 we only considered individuals with at least five sightings (N = 538 individuals).

327 We ran the simulations with parameters s = 14 (selected by trial and error) and set the number of
328 learners to 18 (which corresponds to the actual number of shellers at a cut-off point of five sightings
329 in the empirical data set), and tested for the power of NBDA to detect social learning for cut-offs 5-
330 20. A cut-off point of 11 yielded highest statistical power, with an acceptable level of false positives
331 (= 1.3% at 5% significance level).

332 ## Association strengths

333 Dyadic association strengths were calculated considering individuals that were part of the group
334 within the first five minutes of each encounter and with at least 11 observations but disregarding re-

sightings of the same group (or a subset thereof) within two hours of the initial encounter. We calculated association strengths using the 'simple ratio index' (SRI; Data S1 B), which ranges from 0 (never seen together) to 1 (always seen together) [71], using R package 'asnipe' [72].

Calculations of home range overlaps

Diffusion of a foraging skill, like shelling, might follow an association network simply because individuals that spend time together also experience the same environments. Being subject to the same environmental conditions, individuals would thereby tend to asocially learn the same foraging skills. If this were the case, a network of similarity in environmental usage would be a better predictor of the pattern of diffusion than the social network, since individuals who do not spend time together but utilize the same environments would be similarly predisposed to learn the skill. Therefore, unless environmental usage and the social network are highly correlated, one can distinguish between alternatives and/or quantify the relative influence of each. We used dyadic home range overlap as a proxy for the extent to which two individuals experience the same environmental conditions. For each individual with at least 11 sightings, a home range was defined using 95% kernel density estimates (R package adehabitatHR [73]; Epanechnikov kernel), using a customized smoothing factor based on the reference bandwidth (*href*), which is defined as

$$href = \sigma * n^{-1/6}$$

where $\sigma = 0.5(\sigma_x + \sigma_y)$.

As *href* was found to overestimate home ranges [40], we set a lower limit of 1,000 and an upper limit of 4,000 and then calculated a customized smoothing factor for each individual as

$$h = 0.5(href) + 1{,}500$$

where 1,000 ≤ href ≤ 4,000.

To remove land from the estimated home ranges, we multiplied each individual's home range with a grid of 100 m resolution with values of 0 (for land) and values of 1 (for water), and re-weighted grid cells within each individual's home range to ensure the overall probability of finding an individual

within its home range was equal to 1 [40]. We calculated dyadic home range overlap (95%) using the 'utilization distribution overlap index' (UDOI [74]) using R package adehabitatHR [73] (Data S1 C).

Quantification and Statistical Analysis

NBDA: networks and individual-level variables

Analyses were run using the NBDA package v0.6.1 [19] in R 3.5.2 [75]. We applied multi-network NBDA [4] to our data to assess the importance of social learning on the spread of shelling, while accounting for the importance of environmental factors (measured as dyadic home range overlap), as well as a potential genetic predisposition (measured as dyadic biparental relatedness). NBDA estimates the influence of social transmission based on how closely the pattern of diffusion follows a social network (here an association network). However, it could be that individuals who associate a) tend to have high genetic relatedness, and b) are exposed to similar environmental influences since they inhabit similar spatial regions, thus having a similar rate of asocial learning, which might be mis-identified as social transmission. Whilst we can statistically control for specific, measurable variables (e.g. average water depth) as ILVs [21], there may be unknown/immeasurable influences that cannot be included as ILVs. We therefore included networks quantifying a) the extent to which each dyad is genetically similar and b) the overlap in their home ranges, to quantify the extent to which they experience similar environmental variables.

We applied the 'order-of acquisition diffusion analysis' (OADA) using the three networks, while additionally including several ILVs with potential influence on an individual's rate of acquisition, namely: an individual's sex (-0.5 for females, 0.5 for males, 0 for unknown sex), which was determined genetically or, for adult females, by the presence of a dependent calf; the number of times each individual had been seen (to control for spurious effects of frequently sighted individuals being more likely to be observed with shells); the average water depth of each individual's sightings (as a proxy for habitat use); the average group size (= an individual's average number of group members); and matriline membership as a factor (reduced to 3 levels: haplotypes E, D and other; Data S1D).

In our analysis, we wished to allow for the possibility that shelling might be vertically transmitted to some degree. However, our record of parentage and of shelling status was not sufficiently complete to allow us to model a vertical transmission pathway directly (as per Wild et al [40]). As foraging skills that are learned vertically show an association with haplotype, which is also maternally inherited, the inclusion of haplotype as a factor in the analysis can be used as a proxy for the prevalence of shelling within certain matrilines and, with it, presumable vertical learning.

Haplotypes A, B, D, E, H, F, I and K were identified in the population. However, including 'haplotype' as an 8-level factor is not feasible, given the number of acquisition events observed, since it would result in model overfitting. The factor would also be heavily penalized by AICc. We would also not expect all levels of haplotype to differ in their propensity to learn shelling, rather we would expect one or a few haplotypes to show an enhanced propensity to learning shelling due to its presence in the associated matriline. Here, our aim was to allow for any confounding effects of vertical transmission. Consequently, we reduced the levels of 'haplotype' to better reflect the potential effects of vertical transmission. It seems clear that Haplotypes E and D had the strongest association with shelling, possibly followed by H. Therefore, we tried two versions of the variable, and ran the full set of NBDA models that included haplotype with each, allowing us to obtain the relative support for each version. The first version with four levels (haplotype E, haplotype D, haplotype H and other haplotypes (A, B, I, K, F)) received 8.1% support, whereas the three-level version of haplotype (haplotype E, haplotype D and other haplotypes (A, B, I, F, K, H)) received 88.8% support. We therefore based our inferences on analyses using the three-level version of haplotype.

The (social transmission) parameter *s* is estimated relative to a baseline rate of asocial learning. Continuous variables were standardized to have a mean of 0, such that *s* is estimated relative to the asocial learning rate for an individual with mean values for all such variables. The baseline asocial learning rate was set to the midpoint of males and females, and for Haplotype E, since this resulted

410 in a more stable parameterization of the model, and more easily interpreted estimates for *s*
411 parameters.

412 Previous studies using NBDA with the inclusion of ILVs have selected between an 'additive' model, in
413 which the ILVs affect only the rate of asocial learning, and a 'multiplicative' model, in which the ILVs
414 all affect both asocial learning and social transmission in the same way. In most published cases so
415 far, either the additive or multiplicative data has been strongly favoured by the data, justifying the
416 use of that model for inference. In cases where support has been equivocal, the key results have
417 been found to be robust to selection of the additive or multiplicative model. However, we found that
418 different networks were favoured by the additive model (social association network) and
419 multiplicative model (environmental home range overlap). Whilst the additive model was favoured,
420 the difference in support was not large enough for us to be confident in the result.

421 We therefore used an approach, suggested in [76], fitting a more general 'unconstrained' model, in
422 which the effects of each ILV on asocial and social learning are estimated as independent
423 parameters. Thus, we allow for the fact that i) some variables might influence social learning without
424 forcing the model to assume that all variables do so; and ii) variables might have a different effect on
425 asocial and social learning.

426 We fit models with every combination of ILVs affecting social and asocial learning, and every
427 combination of the three networks resulting in 7,200 different models. Support for each model was
428 calculated using AICc [24]. This allowed us to derive the support for each combination of networks,
429 and for each ILV. Models with a large number of parameters (n = 123) could not be fitted and were
430 dropped from the analysis. This is not surprising, since we would expect some combinations of
431 variables to result in over-parameterized models given the low number of acquisition events. Such
432 models, if they could be fitted, are highly unlikely to yield a favourable AICc and, thus, dropping
433 these models is unlikely to affect our conclusions.

Model averaging methods were used to provide a more stabilized inference about the strength of the transmission parameter for the three different networks and the influence of ILVs on the social and asocial acquisition of shelling. For model averaging (Table 1), we used weighted medians because in OADA, extreme values can badly skew weighted means, even in models with a very small model weighting. Thus, we used weighted medians as a more robust estimate.

We found that standard errors could not be reliably obtained, probably because too many of the key parameters had a highly asymmetrical profile likelihood. For example, for the effect of social transmission, we have more information about the lower bound of the effect than the upper bound. This also makes standard errors misleading measures of precision, as they may be large due to the uncertainty about the upper bound, obscuring the high degree of confidence in the lower bound. This prevents use of a full model-averaged approach in which one presents unconditional standard errors as a measure of precision [24]. Instead, we derive 95% confidence intervals using profile likelihood techniques [77] based on the best predictive model.

Legends for supplemental videos and data

Video S1: Shelling – a foraging innovation in dolphins, Related to STAR Methods

'Shelling' involves the pursuit of prey into large, empty shells of giant gastropods, the Australian trumpet snail (*Syrinx aruanus*) and northern bailer (*Melo amphora*).

Data S1: Input data for running NBDA on the dolphin foraging behavior shelling, Related to STAR Methods

This file contains a matrix with genetic relatedness among individuals (sheet A), an association matrix based on the simple ratio index (sheet B), a matrix depicting dyadic home range overlaps (sheet C), and a list of dolphins' individual level variables (sheet D).

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